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Survey of the butterflies of the Sutter Buttes, California

Melissa R.L. Whitaker[1,2] and Elizabeth C. Long[1,3] *

[1]Graduate Group in Ecology, Center for Population Biology, Department of Evolution and Ecology, University of California, Davis, 1 Shields Ave, Davis CA 95616

[2]Current address: Museum of Comparative Zoology, Harvard University, 26 Oxford St, Cambridge MA 02138

[3]Current address: Dept. of Natural Sciences, Embry-Riddle University, 3700 Willow Creek Rd., Prescott, AZ 86303

mrlwhtaker@gmail.com, eclong@ucdavis.edu

Abstract. The Sutter Buttes are a small, isolated mountain group in the center of northern California's Central Valley. Their location, nearly equidistant between the Coast Range and Sierra Nevada, make the Buttes biogeographically unique. Due to a history of private ownership public and scientific access to these mountains has been limited and much remains to be known about the natural history and ecology of the area. A previous survey of Sutter Buttes butterflies recorded surprisingly few species, and was suspected to represent an incomplete record of the butterfly diversity of the area. In order to assess the accuracy of this survey and explore the biogeographic relationships of the butterflies of north-central California, we performed surveys of the butterfly fauna of the Sutter Buttes. Over two years we performed bi-weekly transects and recorded species presence, abundance, and phenology as well as information about common butterfly host plants found there. Utilizing comparisons of transect data from the Coast and Sierra Nevada Ranges we found that the Sutter Buttes butterfly fauna more closely resembles the Central Valley floor fauna than that of either nearby mountain range. Our results also indicate that the Sutter Buttes harbor a significantly depauperate butterfly fauna: several butterfly species that are common at sites in the Central Valley, Coast Range, or the Sierra foothills are not present in the Sutter Buttes. We discuss possible reasons for these absences, including fire regime, host plant abundance, and nectar availability, and present

Key words: faunal survey, Sutter Buttes, island biogeography, California Central Valley

Introduction

The Sutter Buttes are considered to be the world's smallest mountain range. Located at 39.22 N 121.8 W, they rise from an elevation of 60 meters above sea level in California's Central Valley floor to 645 meters at their highest point, with several peaks over 480 meters (Hausback *et al.*, 2011). The Buttes were formed during a period of Pleistocene volcanism approximately 1.4-1.6 million years ago (Williams & Curtis, 1976). They are nearly circular, and are located almost equidistant from the Coast Range to the west and Sierra Nevada mountains to the east (Fig. 1). This combination of young age and insular location makes the Sutter Buttes interesting biogeographically, though for historical reasons much remains to be known about the ecology of the area.

The Coast Range and Sierra Nevada Range are good candidate source communities for the Sutter Buttes butterfly fauna. They share similar geology, climate, and floral and faunal communities with localities at similar elevations in the nearby ranges. The Central Valley, which lies between the two mountain ranges and surrounds the Sutter Buttes, is very different from either mountain range in terms of geology, climate, and butterfly community composition. For this reason it could be predicted that the Sutter Buttes butterfly fauna should differ from that of the Central Valley and be more similar to one or both nearby mountain ranges. In addition, since the Sutter Buttes are younger than the nearby ranges, colonization is more likely to be in the direction of immigrants to the Sutter Buttes rather than emigrants from the Sutter Buttes to either

* Both authors contributed equally to this manuscript

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nearby range (Schoenherr, 1992). A major aim of this study was to look for evidence of source communities from either the Coast Range, Sierra Nevada Range, or Central Valley floor.

The Sutter Buttes experience a Mediterranean climate characterized by long, hot summers and short, wet winters. The interior of the range receives an average annual precipitation of 51 cm, typically between December-February, compared to the surrounding valley floor, which receives 38 cm. The major ecosystem types of the Sutter Buttes are grasslands, chaparral, and oak woodland, with scattered wetland areas (Schoenherr, 1992). Prior to European colonization the surrounding Sacramento Valley was composed largely of tule marsh and underwent frequent flooding from the Sacramento River, the Feather River, several creeks from the Coast Range, and creeks from the Sierra Nevada. Most of the waterways have since been dammed, the valley drained, and the land developed for agriculture. See Anderson (1983, 2004) for a thorough review of the natural history and ecology of the Sutter Buttes.

While there are not believed to have been permanent human settlements in the Sutter Buttes prior to European colonization, several indigenous groups are known to have utilized the range for foraging, hunting, and cultural and religious reasons. The lands of three tribes, the Valley Maidu or Koncow to the north; the Valley Nisenan or Southern Maidu to the southeast; and Valley Patwin or the Wintun to the west and southwest, overlap at the Sutter Buttes. The largest impact of these indigenous peoples was likely their use of periodic fires for the purpose of native game and food plant management (Kroeber, 1925; Anderson, 2004). As with much of California, the region underwent early settlement by European trappers in the 1820's-1830's, followed by miners in the latter half of the century. The Sutter Buttes themselves were settled by Europeans in the late1800's and early 1900's for the purpose of grazing sheep and cattle, a practice that continues there today. The majority of the Sutter Buttes have remained privately owned since their European settlement, with public and scientific access limited or non-existent during the past half-century (Anderson, 1983). In recent years some private landowners have formed a partnership through the Middle Mountain Foundation to provide programs to promote public education and increase scientific access within the Buttes.

The purpose of this paper is to contribute to the current state of knowledge of the natural history and ecology of the Sutter Buttes by conducting regular surveys of the butterfly fauna present there. This survey aimed to record species presence, abundance, and phenology as well as host plant availability. In doing so

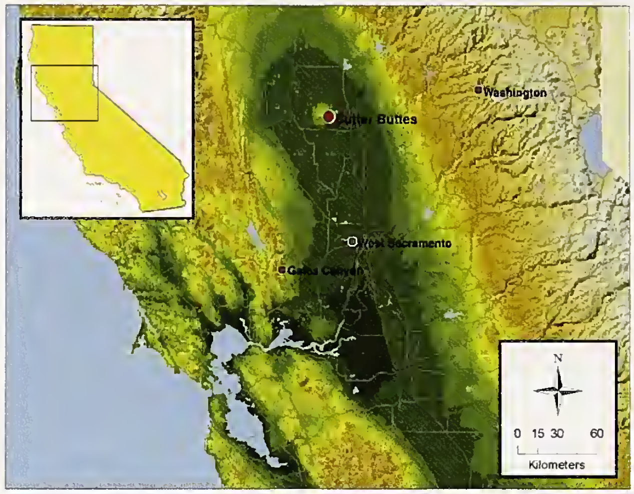

Figure 1. Location of comparison sites relative to Sutter Buttes, adapted from www.butterfly.ucdavis.edu

we hoped to improve on a previous butterfly survey of the Sutter Buttes conducted over 30 years ago (Peoples, 1978, unpub. ms). Because Peoples found only 44 butterfly species (Table 1), a surprisingly small number relative to what might be expected based on the location of the Sutter Buttes, Peoples' survey was suspected to represent an incomplete documentation of the total butterfly diversity of the area. Additional aims of our study were therefore to assess the previous survey's accuracy, explore possible reasons why the Sutter Buttes might support such a depauperate butterfly fauna, and investigate whether observed regional declines are also detected in this isolated location.

Methods

Study Site

This survey was conducted on the Dean Ranch property of the Sutter Buttes with the landowner's permission. This property has been family owned for over 100 years and is used primarily for grazing cattle and cultivating hay. The landowners have been instrumental in promoting educational and scientific access to the area, and much of the natural history information currently available about the Sutter Buttes has come from studies conducted on this site. Though there are structures and primitive roads on the property, much of Dean Ranch remains undeveloped and includes a variety of native ecosystem types. The site includes oak scrubland, a riparian corridor, grazed pasture, cultivated fields, and chaparral, and the terrain includes several hills, a large ridge, and is bordered to the north by the North Butte (Fig. 2).

Table 1. Species recorded at the Sutter Buttes and/or at the three comparison sites. Species recorded in the Sutter Buttes by Peoples, 1978 (SB1). Species recorded in the current study at the Sutter Buttes (SB2); Gates Canyon (GC); Washington (W); and West Sacramento (WS). '*' denotes species for which voucher specimens were collected in the current study (SB2); '#' denotes species for which the larval host plant is absent from the Sutter Buttes. Species in the family Hesperiidae were not included in comparison analysis. The total number of species counted during the current Sutter Buttes survey is included in the final column (Counts (SB2)). Counts are not available for Peoples' 1978 survey (SB1).

Family	Subfamily	Species	Site Presence	Counts (SB2)
Hesperiidae				
	Hesperiinae	*Atalopedes campestris* Boisduval 1852	SB1, SB2, W, WS, GC	NA
	Hesperiinae	*Hylephila phyleus* Drury 1773	SB1, SB2, WS, GC	NA
	Hesperiinae	*Lerodea eufala* Edwards 1869	SB1, SB2, W, WS, GC	NA
	Hesperiinae	*Ochlodes agricola* Boisduval 1852	SB1, SB2, W, GC	NA
	Hesperiinae	*Ochlodes sylvanoides* Boisduval 1852	SB1, SB2, W, GC	NA
	Hesperiinae	*Poanes melane* Edwards 1869	SB1, SB2, WS, GC	NA
	Pyrginae	*Erynnis propertius* Scudder & Burgess 1870 *	SB1, SB2, W, GC	NA
	Pyrginae	*Erynnis tristis* Boisduval 1852	SB1, SB2, W, WS, GC	NA
	Pyrginae	*Heliopetes ericetorum* Boisduval 1852 *	SB1, SB2, W, WS, GC	NA
	Pyrginae	*Pholisora catullus* Fabricius 1793	SB1, SB2, W, WS, GC	NA
	Pyrginae	*Pyrgus communis* Grote 1872	SB1, SB2, W, WS, GC	NA
Lycaenidae				
	Lycaeninae	*Lycaena arota* Boisduval 1852	GC, W	
	Lycaeninae	*Lycaena gorgon* Boisduval 1852	GC, W	
	Lycaeninae	*Lycaena helloides* Boisduval 1852	SB1, GC, W, WS	
	Lycaeninae	*Lycaena xanthoides* Boisduval 1853	SB1, GC	
	Polyommatinae	*Brephidium exilis* Boisduval 1852	WS, GC	
	Polyommatinae	*Celastrina ladon* Cramer 1780	W, GC	
	Polyommatinae	*Cupido comyntas* Godart 1824 *	SB1, SB2, WS, GC	7
	Polyommatinae	*Euphilotes enoptes* Boisduval 1852	W	
	Polyommatinae	*Everes amyntula* Boisduval 1852	W	
	Polyommatinae	*Glaucopsyche lygdamus* Doubleday 1841	GC, W	
	Polyommatinae	*Glaucopsyche piasus* Boisduval 1852	W	
	Polyommatinae	*Leptotes marina* Reakirt 1868	WS	
	Polyommatinae	*Philotes sonorensis* Felder & Felder 1865#	W	
	Polyommatinae	*Plebejus acmon* Westwood 1851 *	SB1, SB2, W, WS, GC	32
	Polyommatinae	*Plebejus icarioides* Boisduval 1852	W, GC	
	Theclinae	*Atlides halesus* Cramer 1777	SB1, SB2, W, WS, GC	2
	Theclinae	*Callophrys augustinus* Westwood 1852	SB1, SB2, W, GC	2
	Theclinae	*Callophrys dumetorum* Boisduval 1852	SB1, W, GC	
	Theclinae	*Callophrys gryneus* Hübner, 1819#	W	
	Theclinae	*Habrodais grunus* Boisduval 1852#	GC, W	
	Theclinae	*Incisalia eryphon* Boisduval 1852#	W	
	Theclinae	*Incisalia mossii* Edwards 1881#	W	
	Theclinae	*Satyrium auretorum* Boisduval 1852	GC	
	Theclinae	*Satyrium californica* Edwards 1862	SB1, W, WS, GC	
	Theclinae	*Satyrium saepium* Boisduval 1852	W, GC	
	Theclinae	*Satyrium sylvinus* Boisduval 1852	W, WS, GC	

Table 1. Continuation.

Family	Subfamily	Species	Site Presence	Counts (SB2)
	Theclinae	*Satyrium tetra* Edwards 1870	GC	
	Theclinae	*Strymon melinus* Hübner 1818	SB1, SB2, W, WS, GC	22
Nymphalidae				
	Danainae	*Danaus plexippus* Linnaeus 1758 *	SB1, SB2, W, WS, GC	15
	Limenitidinae	*Adelpha bredowii* Geyer 1837	SB1, SB2, W, GC	1
	Limenitidinae	*Limenitis lorquini* Boisduval 1852	SB1, SB2, W, WS, GC	5
	Heliconiinae	*Agraulis vanillae* Linnaeus 1758#	GC	
	Heliconiinae	*Speyeria callippe* Boisduval 1852	W	
	Heliconiinae	*Speyeria hydaspe* Boisduval 1869	W	
	Heliconiinae	*Speyeria zerene* Boisduval 1852	W	
	Nymphalinae	*Aglais milberti* Godart 1819	SB1, SB2,	1
	Nymphalinae	*Chlosyne palla* Boisduval 1852	W, GC	
	Nymphalinae	*Chlosyne leanira* Felder & Felder 1860	W, GC	
	Nymphalinae	*Euphydryas chalcedona* Doubleday 1847	W, GC	
	Nymphalinae	*Euphydryas editha* Boisduval 1852#	W	
	Nymphalinae	*Junonia coenia* Hübner 1822 *	SB1, SB2, W, WS, GC	51
	Nymphalinae	*Nymphalis antiopa* Linnaeus 1758	SB1, SB2, W, WS, GC	1
	Nymphalinae	*Nymphalis californica* Boisduval 1852	SB1, SB2, W, GC	4
	Nymphalinae	*Phyciodes mylitta* Edwards 1861 *	SB1, SB2, W, WS, GC	23
	Nymphalinae	*Phyciodes pulchella* Boisduval 1852	SB1, W	
	Nymphalinae	*Polygonia satyrus* Edwards 1869	SB1, GC	
	Nymphalinae	*Polygonia zephyrus* Edwards 1870	GC	
	Nymphalinae	*Vanessa annabella* Field 1971	SB1, W, WS, GC	
	Nymphalinae	*Vanessa atalanta* Linnaeus 1758	SB1, SB2, WS, GC	2
	Nymphalinae	*Vanessa cardui* Linnaeus 1758	SB1, SB2, W, WS, GC	72
	Nymphalinae	*Vanessa virginiensis* Drury 1773 *	SB1, SB2, W, WS, GC	1
	Satyrinae	*Cercyonis pegala* Fabricius 1775	GC	
	Satyrinae	*Cercyonis sthenele* Boisduval, 1852	W	
	Satyrinae	*Coenonympha tullia* Müller 1764	W, WS, GC	
Papilionidae				
	Papilioninae	*Battus philenor* Linnaeus 1771 *	SB1, SB2, W, WS, GC	564
	Papilioninae	*Papilio eurymedon* Lucas 1852	SB1, W, GC	
	Papilioninae	*Papilio multicaudata* Kirby 1884 *	SB1, SB2, GC	2
	Papilioninae	*Papilio rutulus* Lucas 1852 *	SB1, SB2, W, WS, GC	2
	Papilioninae	*Papilio zelicaon* Lucas 1852 *	SB1, SB2, W, WS, GC	1
	Parnassiinae	*Parnassius clodius* Ménétriés 1857#	W	
Pieridae				
	Coliadinae	*Colias eurytheme* Boisduval 1852 *	SB1, SB2, W, WS, GC	124
	Coliadinae	*Zerene eurydice* Boisduval 1855 *	SB1, SB2, W, GC	1
	Pierinae	*Anthocharis lanceolata* Lucas 1852	W	
	Pierinae	*Anthocharis sara* Lucas 1852 *	SB1, SB2, W, GC	8
	Pierinae	*Euchloe ausonides* Lucas 1852	SB1, GC	
	Pierinae	*Euchloe hyantis* Edwards 1871#	W	

Table 1. Continuation.

Family	Subfamily	Species	Site Presence	Counts (SB2)
	Pierinae	*Neophasia menapia* Felder & Felder 1859	W	
	Pierinae	*Pieris oleracea* Harris 1829	W, GC	
	Pierinae	*Pieris rapae* Linnaeus 1758 *	SB1, SB2, W, WS, GC	28
	Pierinae	*Pontia protodice* Boisduval & Leconte 1830	WS, GC	
	Pierinae	*Pontia sisymbrii* Boisduval 1852	W, GC	
Riodinidae				
	Riodininae	*Apodemia mormo* Felder & Felder 1859	W	

Transect

We conducted biweekly Pollard walks (Pollard, 1977) from March 2008 to March 2010, between 10:00-16:00 on days when weather was suitable to permit butterfly activity (typically 18-37° C, partial to full sun, low wind). A transect of 5-8 kilometers was surveyed which included several important habitat types, including riparian areas, hilltops, south-facing slopes, rocky outcroppings, and weedy fields (Fig. 2).

Butterflies were identified in flight, and some specimens were collected as vouchers. A total of 47 vouchers were taken, which are housed at the UC Davis Bohart Museum of Entomology. Many of the hesperiid species observed at the Sutter Buttes were located behind locked pasture gates and could not be captured or identified by eye; therefore the species list for Hesperiidae is almost certainly incomplete. We included them in the faunal survey only when they could be collected for identification, and we excluded members of the Hesperiidae from our analyses. To assess the likelihood that our survey recorded the majority of the butterfly species present in the Sutter Buttes, a randomized species accumulation curve (Gotelli & Colwell, 2001) was constructed using the 'Vegan' package in R (Oksanen *et al.*, 2011; R Development Core Team, n.d.)) Using the same package, the Chaol estimator was calculated in order to extrapolate the expected species richness in our study area (Colwell & Coddington, 1994). We employed sample-based species accumulation curves as an alternative to individual-based methods, which are known to over-estimate species richness when individuals are patchily distributed (Gotelli & Colwell, 2001). Species names conform to Pelham (2008).

Data were compared to faunal records from similar sites in the California Coast Range (Gates Canyon, 150-670 m a.s.l.) and the Sierra Nevada Range (Washington, 760 m a.s.l.) as well as the Central Valley floor (West Sacramento, 7 m a.s.l.; Fig. 2). Data from comparison sites were collected under similar conditions and during the same time period by A.M. Shapiro as part of an ongoing butterfly monitoring study (http://butterfly.ucdavis.edu).

Similarity Indices

A Chao-Soerensen index of similarity (C-S index) was calculated for the Sutter Buttes and each of the 3 comparison sites presence-absence data, implemented in R using the Fossil package (Vavrek, 2001). The Chao-Soerensen measure was selected in order to reduce the impact of under-sampling caused by traditional similarity indices (e.g. Jaccard index; Jaccard, 1912). Abundance data were not available for all surveys; therefore, presence/absence per site visit was used as a proxy for abundance (e.g., species "A" was seen 21 of 46 times at site 1, and 1 of 20 times at site 2).

In addition to calculating the C-S index for the Sutter Buttes and each comparison site we looked for shared unique species (SUS), defined as species found at the Sutter Buttes and only one of the three comparison sites during the study period.

After identifying species that were present at one or more of the comparison sites, but absent from the Sutter Buttes, we investigated host plant presence/absence for these missing species. We compared known host plant requirements for each missing butterfly species against Sutter Buttes floral records from Anderson (2004), the CalFlora database (2008), and our own observations.

The Papilionoidea species list from this survey was compared to the 1978 survey performed by Peoples (Table 1). Species absent from either survey were noted in order to assess the accuracy of Peoples' survey and to explore changes in butterfly faunal composition of the region since 1978.

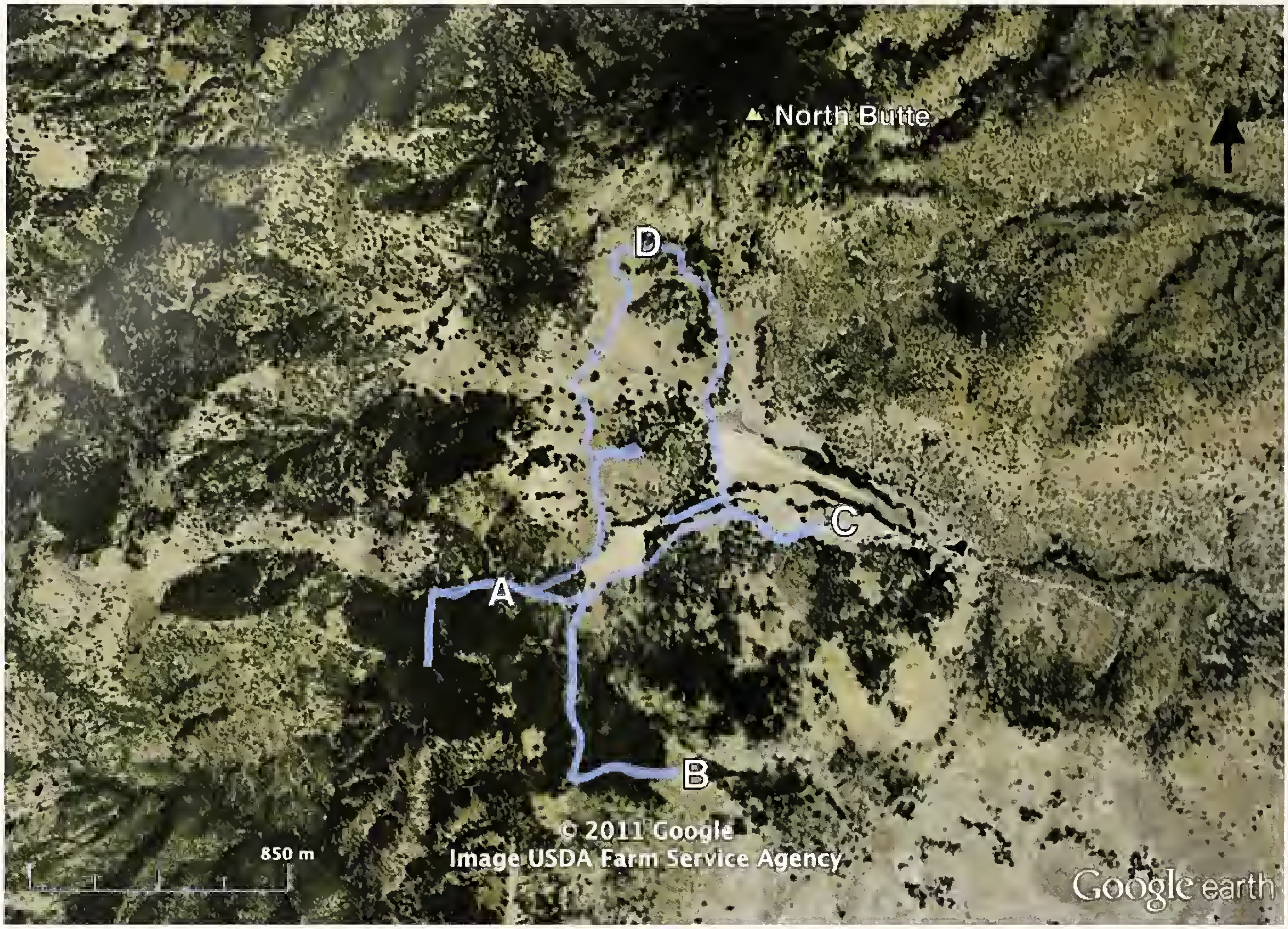

Figure 2. Survey transect with key sites labeled. **A**: Riparian corridor, **B**: High peak where hilltopping was prevalent, **C**: Dean's Ranch homestead, **D**: Chaparral/rocky outcroppings

Results

Species Presence/Absence

A total of 30 species were recorded in this survey at the Sutter Buttes study site, including 24 Papilionoidea species comprising four families and eight sub-families (Table 1). The species accumulation curve for Papilionoidea (Fig. 3) and the value of the Chao1 estimator (27.6) suggest that there are several (~3-4) additional species present in the Sutter Buttes that were not recorded in the present survey. During the same time period, the comparison sites recorded 57 species (Washington), 52 species (Gates Canyon), and 25 species (West Sacramento), all Papilionoidea (http://butterfly.ucdavis.edu). A total of 39 species from 5 families and 9 sub-families were present at one or more of the comparison sites but absent in both surveys of the Sutter Buttes (Table 1). Two of those species, *Coenonympha tullia* Edwards 1871 and *Satyrium sylvinus* Boisduval 1852 were present at all three comparison sites, but absent from both surveys of the Sutter Buttes (Table 1). One species, *Aglais milberti* Godart 1819, was recorded at the Sutter Buttes, but not at any of the three comparison sites.

We found *Battus philenor* Linnaeus 1771 to be the most common butterfly species, outnumbering the next most common species (*Pieris rapae* Linnaeus 1758) by more than 3:1. This result was not shared by any of the 3 comparison sites. The remaining 23 Sutter Buttes species were generally found in lower numbers than at the comparison sites for which counts are available.

Butterflies were found throughout the transect in all different habitat types. Although a few species were restricted to only one or two habitats (e.g. *Anthocharis sara* Lucas 1852 was only found in one riparian area) most species were not associated with specific habitats.

Although we did not directly test for it, we did not generally observe phenological differences between species found at the Sutter Buttes and the three comparison sites. The lone exception was *B. philenor*, which was observed at the Sutter Buttes in large numbers until much later in the season (until August-September) than at any of the comparison sites (typically early July).

Site Similarity

Gates Canyon

Of the 52 Papilionoidea species (from 4 families, 11 subfamilies) recorded during the study period at Gates Canyon, 24 were also recorded at the Sutter Buttes. One species, *A. milberti*, was recorded at the Sutter Buttes but not at Gates Canyon. The calculated C-S index was 0.818. Gates Canyon was the only site to record an SUS with the current Sutter Buttes survey: *Papilio multicaudata* Kirby 1884. Two other species, *Lycaena xanthoides* Boisduval 1853 and *Euchloe ausonides* Lucas 1852, were SUS between Gates Canyon and Peoples' Sutter Buttes survey.

Washington

Twenty of the 57 Papilionoidea species (from 5 families, 13 subfamilies) recorded at Washington during the study period were also recorded at the Sutter Buttes. Four species, *A. milberti*, *Cupido comyntas* Godart 1824, *P. multicaudata*, and *Vanessa atalanta* Linnaeus 1758, were recorded at the Sutter Buttes but not at Washington. Washington had the lowest C-S index score of the 3 comparison sites at 0.642. There were no SUS between Washington and the current survey, although one was recorded from Peoples' survey (*Phyciodes pulchella* Boisduval 1852).

West Sacramento

West Sacramento shared 17 of the 24 Papilionoidea species (from 4 families, 10 subfamilies) recorded at the Sutter Buttes. An additional 8 species were recorded at West Sacramento but not at the Sutter Buttes. The C-S index between these two sites was the highest of the three comparison sites at 0.85.

Comparison to Peoples' (1978) survey

Peoples' survey of the Sutter Buttes found 33 Papilionoidea butterfly species (Table 1). There were 9 species found in Peoples' survey that were not recorded in our survey, and no additional species were found that had not already been recorded by Peoples (1978).

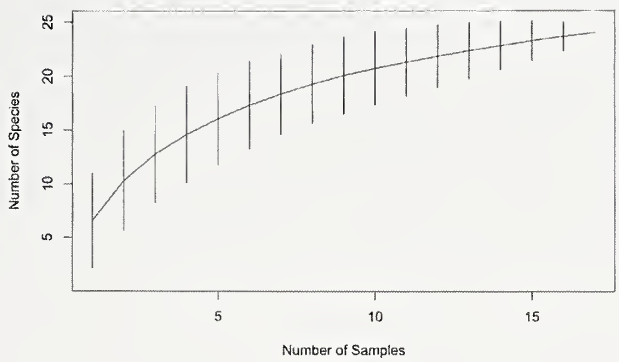

Figure 3. Mean species accumulation curve and its standard deviation based on random permutations of the data. A total of 24 Papilionoidea species were recorded. Because the number of species continues to increase with sampling effort, the curve suggests that additional species are present in the Sutter Buttes but were not recorded.

Host plant presence/absence

Of the species missing from the Sutter Buttes, only 9 could be explained by the co-absence of the larval host plants (Table 1). In the remaining 30 cases at least one host plant species has been recorded within the Sutter Buttes range.

Discussion

Of primary interest to our study was whether there is any indication of a dominant source region for the Sutter Buttes butterfly fauna. The Sutter Buttes are much younger than both the nearby Coast Range and Sierra Nevada Range, suggesting that any species found in either mountain range and in the Sutter Buttes but not in the Central Valley may have colonized the Sutter Buttes from one or both nearby ranges. Because certain species found in the Coast and Sierra Nevada ranges exhibit phenotypic differences, suggesting divergent lineages (e.g. *Euphydryas chalcedona* Doubleday 1847), their presence at the Sutter Buttes would immediately suggest a likely source. Likewise, a high number of SUS would suggest that either the Coast Range or Sierra Nevada Range contributed more to the butterfly fauna of the Sutter Buttes. However, our results indicate that the Sutter Buttes butterfly fauna most closely resembles that of the Central Valley floor despite bearing a stronger geologic and elevational similarity to the foothills of the Coast Range and the Sierra Nevada Range. Only one of the species recorded at the Sutter Buttes during the modern survey was identified as a

SUS (*P. multicaudata* was a SUS with Gates Canyon), and only one species is unique to the Sutter Buttes. That species, *Aglais milberti*, is a seasonal, altitudinal migrant that overwinters at low elevations and migrates to the Sierra Nevada mountains as adults. *A. milberti* was absent from the comparison sites during the timeframe of our survey, though it was last recorded at Gates Canyon in the mid 1990s, at West Sacramento in the late 1980s, at Washington in the early 1990s, as well as occasionally at additional study sites along the Central Valley floor. Based on these findings, there is no evidence to implicate either mountain range as a source population for any of the species at the Sutter Buttes.

Gates Canyon (Coast Range) and Washington (Sierra Nevada Range) shared 24 and 20 species with the Sutter Buttes, respectively. While both of these sites had a higher number of shared species than did the Central Valley site (West Sacramento at 17), both mountain sites had a much higher overall number of species than did the Sutter Buttes (52 and 57, respectively) or West Sacramento (25), resulting in a lower percentage of shared species and lower C-S index scores.

Several of the missing species at the Sutter Buttes are notable because of their otherwise weedy, ubiquitous nature. For example, the two species that were recorded at all three comparison sites (and missing at the Sutter Buttes) are widespread throughout the entire region. Likewise, three of the additional species found at West Sacramento but not at the Sutter Buttes (Table 1) support the suggestion that even several weedy species have been unable to colonize the Sutter Buttes. Based on the species accumulation curve (Fig 3) and the Chao1 value of 27.6 species, we estimate that the present survey recorded approximately 87% of the butterfly species present in the Buttes. The remaining taxa are likely represented by rare, patchily distributed, or seasonally restricted species, making the absence of common and weedy species all the more conspicuous.

Since butterfly species distributions are closely linked to those of their host plants we investigated whether the depauperate butterfly fauna at the Sutter Buttes was linked to the co-absence of larval host plants. We found that of the 39 butterfly species present at one or more comparison sites but absent from the Sutter Buttes, only 9 could confidently be explained by host plant absence. In the other 30 cases, at least one potential host plant has been documented within the Sutter Buttes range (Anderson, 2004; Calflora Database, 2008).

Anderson (2004) points out that many plant species found in the Sutter Buttes are present at low abundance, a pattern we also observed during our survey. For example, while we recorded the presence of *Symphyotrichum subulatum* (Asteraceae), host plant for *Chlosyne palla* Boisduval 1852, it was restricted to one isolated site on the flank of the North Butte, and only a few plants were present. Furthermore, some other plant species were recorded predominantly in the property's riparian corridor; while this is certainly an important habitat, it makes up only a small portion of the total area at the Sutter Buttes. We observed a similar pattern for many butterfly host plants, suggesting that although the necessary plant species are present, their local densities may be inadequate for supporting a permanent butterfly population.

Furthermore, our broad treatment of host plant presence and absence included all acceptable host species, without focused attention to preferred host plants. There is evidence that some butterfly species that utilize multiple host plants may exhibit local specialization (e.g. *Euphydryas chalcedona* Doubleday 1847: Bowers 1986). While we recorded a large number of potential host plants at the Sutter Buttes, it is possible that the absence of preferred host plants has precluded butterfly immigrants from colonizing.

Inadequate abundance of adult nectar sources may also pose an impediment to butterfly colonization at the Sutter Buttes. There is evidence that nectar limitation may have a detrimental effect on butterfly population viability (Schultz & Dlugosch, 1999; Murphy *et al.*, 1984; Boggs, 2003). A number of regionally important nectar sources are absent from the Sutter Buttes. Most notable among them is the California Buckeye tree (*Aesculus glabra*), which is an important late-spring nectar source for a wide variety of butterfly species in this region. The flowers of this tree tend to bloom concurrently with peak spring butterfly flight, and a single tree is commonly visited by dozens of individuals of many species at a time. Other important nectar sources were either absent or present at low abundance, suggesting that nectar availability may be problematic at the Sutter Buttes. We observed anecdotal evidence for nectar limitation during our surveys. For example, we often found large numbers of *B. philenor* attempting to nectar on blackberry flowers (*Rubus* spp.). This is a very unusual behavior, as blackberries are bee-pollinated and likely do not produce substantial quantities of nectar for butterflies, suggesting inadequate local availability of preferred nectar sources.

Peoples' 1978 survey of the area around the South Butte (~3km from our transect site) recorded 33 Papilionoidea species, a surprisingly low number relative to what might be expected for this region. While it is possible that Peoples' list represents an incomplete account of the butterfly species richness in the Buttes, we are unaware of any additional species being recorded at the Sutter Buttes in the time since her survey was conducted. Not only did our recent study fail to record additional species, we recorded 9 fewer species than did Peoples' survey, and estimated a total richness of ~5 fewer species (Chao1 = 27.6). Since the two studies were conducted on different properties within the Sutter Buttes it is possible that the species recorded by Peoples are not all present in our study area, or that they are present in our area but were not recorded. Alternatively, it is possible that some species have been extirpated from the Sutter Buttes in the ensuing years since Peoples' study. Similarly, although host plants have been recorded for many of the 'missing species' at the Sutter Buttes, we cannot assess the actuality of records that were not confirmed by our own observations, and it is possible that some plants have gone locally extinct from the Sutter Buttes since they were recorded. Although data were not available for comparison sites during the time corresponding to Peoples' survey (thus precluding the possibility of calculating similarity indices for Peoples' data) we interpret the results of the present survey as indicative of a possible decline in butterfly species richness at the Sutter Buttes in the time since Peoples' survey. While we cannot explain with certainty why butterflies in the Sutter Buttes might be in decline, Forister *et al.* (2010, 2011) have observed similar declines in butterfly species richness at sites in the Central Valley over the past 2-3 decades related to land-use change and climatic warming. Specifically, they found that 7 of the 9 species found in Peoples' survey but not the current survey were also declining at one or more Central Valley survey sites; the remaining two species, *Phyciodes pulchella* and *Papilio eurymedon* were not recorded at all at their Central Valley survey sites.

An additional impediment to butterfly colonization and persistence may be wildfire (Anderson, 2004). Most ecological communities in California are adapted to—and in fact benefit from—periodic wildfires. The grassland, oak woodland, and chaparral habitats of the Sutter Buttes are all examples of fire-adapted communities. It is likely that prior to European colonization, periodic fires burned portions of the Sutter Buttes without devastating effect. These fires are believed to have moved slowly through a mosaic habitat of burned and unburned areas, leaving butterfly and host plant refugia intact (Schoenherr, 1992). It is likely, however, that because of the Sutter Buttes' small size and relative isolation, fewer refugia are available in the Buttes, making butterflies and/or host plants more susceptible to large fires (or other environmental hazards) than species in the comparison sites. Furthermore, modern fire suppression policies have significantly altered the impact of fire in many ecosystems. Many of the fires that occur now often move through an area much more quickly, burn much hotter, and do more damage than the wildfires prior to European settlement (D'Antonio & Vitousek, 1992). A number of fires in modern times may have had an effect on wildlife in the Sutter Buttes. Several arsons burned large areas within the range in the 1960s (Anderson, 1983), and grass fires are always a possibility during drought years and throughout the summer dry season. During our study period a grass fire, believed to have originated at an electrical transformer, occurred near the South Butte. While we did not directly observe negative effects to the butterfly fauna from this fire we can not discount the possibility that host plants were destroyed or butterflies directly killed, including species of either that we did not record during our study.

While the Sutter Buttes are a truly remarkable mountain system in terms of their small size and isolation from other mountain ranges, there are several examples of larger but relatively isolated mountains across the world. Often deemed "sky islands," these mountains are characterized by physical separation from other, more continuous, mountain ranges, and by being surrounded by "seas" of lowlands consisting of dramatically different climates and environments. Sky islands are of great bigeographical and conservation significance as they often harbor relictual and/or endemic populations, and can provide important opportunities for vertical migration and environmental refugia in response to climate change (Forister *et al.*, 2010). Ideally, this study would compare our findings to butterfly surveys from other sky islands, though to our knowledge comprehensive surveys and comparative biogeographical investigations are often severely lacking in other isolated mountain systems, and the systems that are well-studied are not directly comparable to the Sutter Buttes. For example, the Madrean sky islands in southeastern Arizona are some of the best studied of the world's sky island ecosystems and the most geographically proximate to the Sutter Buttes. These mountains harbor well over 200 species of butterflies (Stewart, 2001; Bailowitz, 2007), a great deal more than our estimate for the Sutter Buttes, but are also much older, taller, larger, and less isolated than the Sutter Buttes (Drewes, 1972), making direct comparisons uninformative.

Faunal investigations of the world's sky islands are of the utmost importance considering the rapid loss of biodiversity worldwide, changes in regional climate, and land use change. We hope that this butterfly survey of the world's smallest mountain range will inspire similar surveys and biogeographical analyses of other sky islands to elucidate the patterns and processes that determine faunal composition in isolated ecosystems.

Conclusions

The present survey found the butterfly fauna of the Sutter Buttes to be surprisingly species-poor. In comparison to sites in the Central Valley, Coast Range, and Sierra Nevada Range, the composition of Sutter Buttes' butterfly fauna is most similar to that of the Central Valley floor, despite bearing more ecological and elevational resemblance to the mountain sites. Results from the present study were compared to a previous butterfly survey and suggest a decline in species richness in the Sutter Buttes since 1978, in keeping with regional declines observed by Forister *et al.* (2010, 2011). While we explored host plant availability, nectar availability, and fire history as possible explanations for the impoverished fauna at the Sutter Buttes, more detailed biogeographical, historical, and/or climatic analyses will be necessary to understand the ecology and biogeography of butterfly populations in this unique mountain range.

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